

Carbon and Nitrogen Stable Isotope Assessment of the Lake Roosevelt Aquatic Food Web

Abstract

The purpose of this study was to investigate the carbon and nitrogen stable isotope signatures of the common aquatic organisms in Lake Roosevelt, a large volume storage reservoir in the upper Columbia River where annual water level fluctuations limit benthic and littoral productivity and diversity. Carbon isotope signatures were used to indicate the relative importance of benthically versus pelagically fixed carbon in each species diet. Nitrogen isotope signatures were used to identify the trophic level occupied by each species. We expected a limited benthic component in the aquatic community and a need for benthic fishes to use a high proportion of pelagically fixed carbon. Distinct pelagic versus benthic carbon signatures were detected for primary producers and primary consumers (benthic organisms possessed greater ^{13}C), which meant that the relative importance of the two carbon sources in the diet could be determined. Our collections revealed few benthic organisms, and of those, only one trophic level of benthic consumers was detected from isotope data. Most of the animal diversity in Lake Roosevelt utilizes pelagically fixed carbon. Even those fishes that are usually considered obligate benthivores (cyprinids, catostomids, and cottids) collected more than 65% of their carbon from pelagic sources.

Introduction

This study investigated the importance and fate of open-water (pelagic) versus near-shore (benthic) primary productivity in the Lake Roosevelt reservoir of the Columbia River, Washington. Our purpose was to track benthic and pelagic carbon flow through the food web to determine the predominant carbon sources for consumers. Stable isotope analysis was chosen for its ability to discern between benthic and pelagic carbon in organism diets (France 1995), and the ability to determine relative trophic status of organisms (DeNiro and Epstein 1981).

Typical lake and reservoir systems have diverse benthic and pelagic communities of primary producers. Fixed carbon arising from both attached benthic algae (periphyton) and planktonic algae (phytoplankton) enters the food web and is passed between consumer level organisms. Lake Roosevelt, Washington, however, undergoes an annual drawdown more extreme than most reservoirs, which effectively eliminates benthic carbon fixation for the duration of the drawdown (Beckman et al. 1985). The reservoir is drawn down an average of 15 m beginning in January and does not return to full pool until mid-July

(Nigro et al. 1981). At the peak of the winter drawdown the water level is below the level of the previous summer and autumn euphotic zone, eliminating virtually the entire littoral community of the reservoir. Benthic productivity does not begin until early summer because littoral organisms cannot overwinter in the reservoir, and macrophytic plants and algae that begin to recolonize at the winter low water mark find themselves below the euphotic zone once the water level is returned to normal in July. Significant benthic production may not occur until well into August.

Nearly all fishes in Lake Roosevelt are supported by zooplankton for at least a portion of their lives, usually as juveniles. As adults, these fishes vary between obligate pelagivores, benthivores, or some combination of both. Lake Roosevelt contains several species of fishes that are typically considered in most systems to be obligate benthivores (Wydoski and Whitney 1979, Simpson and Wallace 1982). These include carp (*Cyprinus carpio*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*Catostomus columbianus*), and sculpins (*Cottus* sp.). In a system with limited benthic production, we questioned whether these fishes truly functioned as obligate benthivores, or whether they would be forced to a partially pelagic diet. Stomach content data collected annually from Lake Roosevelt fishes indicated a high benthic diet in these fishes (Peone

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et al. 1991, Griffith and Scholz 1991, Cichosz et al. 1998, Baldwin and Polacek 2002.) However, the majority of the fish collection for stomach analysis occurs in the late summer months when benthic productivity is at its highest, which may give the appearance that fishes are feeding more heavily from the benthic region than they really are. By using stable isotope analysis, we examined food sources over time periods from months to years, which integrated periods of high and low benthic productivity.

Benthic carbon entering the food web can be distinguished from pelagic carbon by periphyton's significant enrichment in $\delta^{13}\text{C}$ over phytoplankton (France 1995). An organism's stable carbon isotope ratios reflect the isotope ratios of its prey (DeNiro and Epstein 1978) therefore, incorporation of either benthically or pelagically produced carbon can be detected in the $\delta^{13}\text{C}$ values of consumers (Keough et al. 1996). Organisms with both benthic and pelagic carbon in their diet will have $\delta^{13}\text{C}$ values between those of benthically and pelagically fixed carbon (Peterson and Fry 1987).

Relative trophic status of an organism can be detected by a 3-4‰ increase in $\delta^{15}\text{N}$ between prey and predator (DeNiro and Epstein 1981, Minagawa and Wada 1984, Hobson and Welch 1992, Cabana and Rasmussen 1994). With each trophic level increase, a percentage of carbon is lost to feces, metabolism, and specific dynamic activity (Odum 1957). If benthic primary production is minimal in Lake Roosevelt, benthic carbon should become noticeably diminished as carbon is lost from the food web (O'Brien 1990). Depending on food availability, fishes will adjust their diets, in turn altering their stable isotope values (Vander Zanden et al. 1999a). In this case benthically feeding fishes will be forced to a more pelagic diet. The effect that this will have on the isotope ratios of these fishes is that as $\delta^{15}\text{N}$ increases, $\delta^{13}\text{C}$ should shift toward pelagically derived carbon resulting in relatively lower $\delta^{13}\text{C}$ values.

The reservoir's limited littoral productivity, along with the abundance of fishes commonly known to be obligate or facultative benthivores, provides a unique opportunity to study food web structure. This aim of this study was to trace carbon pathways in the reservoir to determine the degree to which benthic and pelagic primary producers were supplying carbon to the food web. We predicted that there would be a complete set of trophic levels of organisms deriving carbon from

pelagically based primary producers. In the benthic portion of the food web, however, we predicted that organisms would shift towards a pelagic diet with each increase in trophic level. Thus, as $\delta^{15}\text{N}$ increased in benthic organisms, $\delta^{13}\text{C}$ was expected to shift towards the pelagic carbon source. If benthic primary productivity is in fact being reduced, stable isotope analysis should show the depletions of benthic carbon in the food web. We hypothesized that fishes that are commonly known to feed partially or exclusively from the benthos would be forced to shift their feeding to encompass a more pelagic diet, resulting in those organisms having stable isotope ratios indicative of a partially pelagic diet.

Methods

Study site

Lake Roosevelt is a 243 km long reservoir of the Columbia River, located behind Grande Coulee Dam in northeastern Washington (Figure 1). Grand Coulee Dam was completed in 1939 and reached full pool for the first time in 1941. The reservoir inundates 393 km² with a storage capacity of 1.16 X 10¹⁰ m³. At a full pool elevation of 397 m above mean sea level the reservoir has a maximum depth of 122 m, and 1544 km of shoreline. The lower portion of the reservoir flows through shrub step, desert terrain, while the middle and upper regions are located in mountainous regions dominated by ponderosa pine (Wilson 1996). Flow through the reservoir has a water residence time that varies from 15 days in the spring to 83 days in the fall and winter. The annual water temperature varies from 2.2°C in the early spring to 20°C in late summer (Weirenga et al. 1997).

The water level of the reservoir is reduced every spring to serve as a recipient of mountain snow melt. The drawdown typically begins in January, peaks sometime in May, and is returned to full pool by the beginning of July. Draw down events, on average, reduce the reservoir's volume by 55%, surface area by 45%, and mean depth by 7 meters (Beckman et al. 1985). The water level is dropped below the euphotic depth eliminating nearly all littoral and benthic primary producers (Beckman et al. 1985). The drawdown levels have averaged 15 m over the past 15 yr, and have varied from a minimum of 4.3 m to the maximum of 25 m (U.S. Army Corps of Engineers 2000). In 1999, however the water level was reduced by 23 m, making

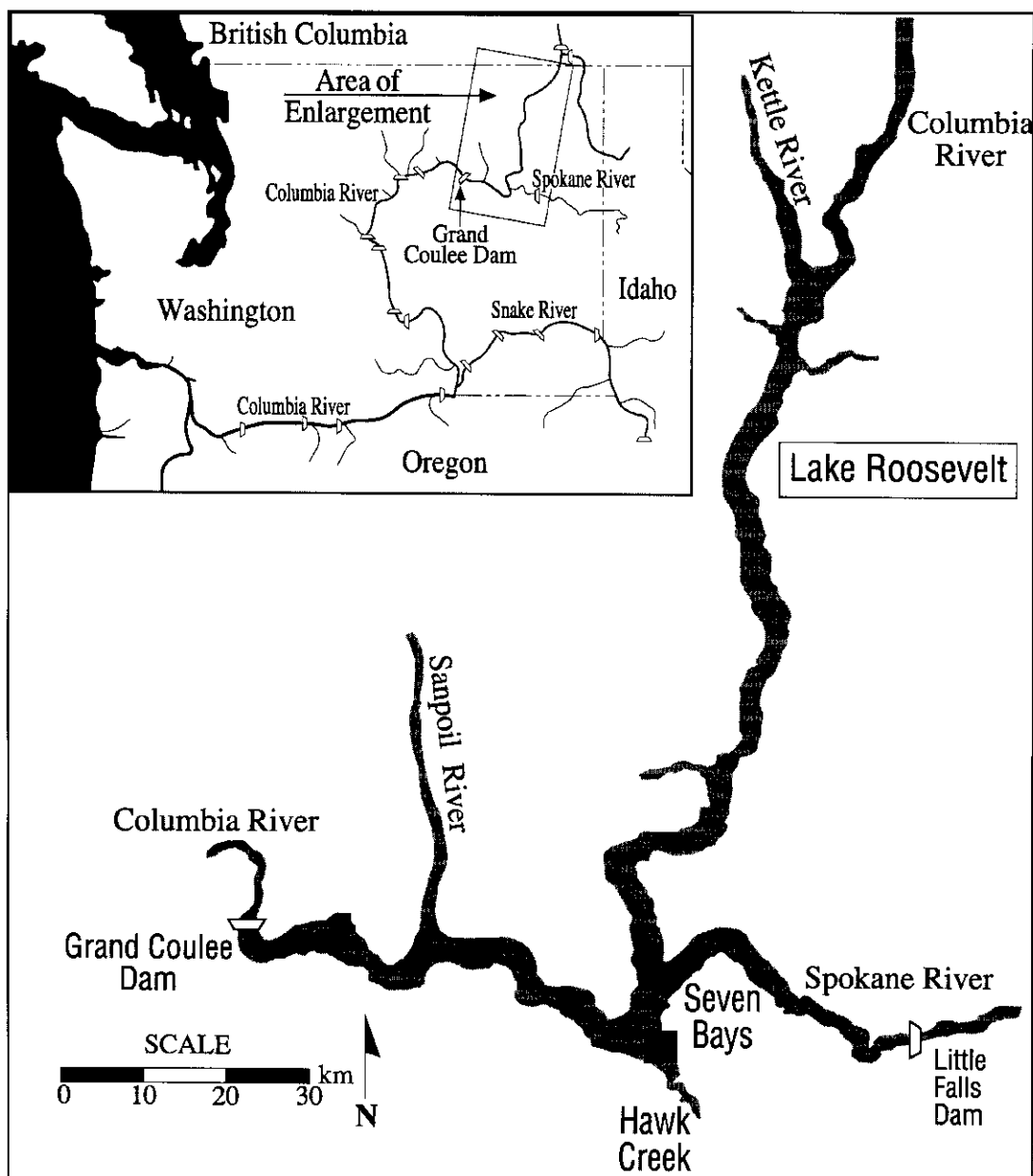


Figure 1. Lake Roosevelt and the collection locations.

it one of the more extreme drawdown events. The 2000 drawdown reduced the reservoir elevation by 17 m making it slightly more extensive than the 15 m average.

All samples were collected from the Seven-Bays and Hawk Creek region of the reservoir (Figure 1). Seven-Bays is named for a series of small bays located on the eastern shoreline. The

bays tend to have sandy shorelines that drop off quickly, allowing little benthic primary production. Hawk Creek enters an estuary of Lake Roosevelt after flowing over Hawk Creek Falls, which are impassable to fishes. The estuarine region is left exposed when the reservoir is drawn down, and becomes colonized with reed canary grass. When the reservoir is brought to full pool

the estuary becomes inundated. The inundated reed canary grass (*Phalaris arundinacea*) then provides substrate for periphyton development.

The Seven-Bays and Hawk Creek region of the reservoir was chosen as the study site due to its relatively high species richness and high concentration of fishes. We predicted that the collection of three feeding groups, including obligate benthic feeders, obligate pelagic feeders, and organisms with mixed benthic and pelagic diets would be possible at this location.

Sample Collection

Samples were collected during the last week of July and the first week of August in 1999 and the first two weeks of August in 2000. Sample collection was limited spatially and temporally to maintain isotopic uniformity. We examined 33 different organisms representative of the Lake Roosevelt food web (Table 1). Phytoplankton were collected from the pelagic region of the reservoir by pumping water from a depth of 1 meter through a 100 μm sieve into 20 L carboys. The majority of the phytoplankton composition consisted of diatoms, with a smaller percentage of green algae and cyanobacteria. The centrifuged phytoplankton pellets were rinsed with deionized water, allowed to resettle, and dried for 24 hr at 60°C.

Periphyton were collected from two locations in the reservoir. A dip net was used to collect periphyton colonizing submerged reed canary grass in the Hawk Creek arm, and in the Seven Bays region it was scraped from substrate suspended at a depth between 1 and 2 m in the open water. The periphyton were rinsed repeatedly with deionized water at the lab to remove colonized invertebrates.

Zooplankton were collected from the pelagic region by vertical hauls with a 0.5 m diameter, 200 μm mesh, conical plankton net. Species were isolated and concentrated using a combination of sieving and hand picking. Chironomids were collected from the sediment and from submerged reed canary grass. An Eckman dredge was used to collect chironomids from the sediment, and a dip net was used to collect them from the reed grass beds, along with corixids, aquatic mites, and snails. Invertebrates were grouped together by taxa and collection site, rinsed with deionized water, dried at 60°C for 24 hr, ground to homogeneity, and sealed in glass vials. Each individual invertebrate

sample was composed of enough individuals to ensure dry mass exceeded five mg.

Fishes were collected with electroshocking boats, backpack electroshocking gear, and vertical and horizontal gill nets. The majority of the adult fishes were collected with the electroshocking boats, while the majority of the young-of-the-year (YOY) fishes were collected with backpack gear. The gill nets were used predominantly to catch lake whitefish (*Coregonus clupeaformis*), kokanee (*Oncorhynchus nerka*) and burbot (*Lota lota*).

A section of dorsal muscle tissue was filleted from each fish for analysis. Fishes too small to be filleted had their heads and viscera removed in preparation for analysis. All samples were rinsed with deionized water, dried at 60°C, ground to homogeneity, and stored in glass vials.

Stable Isotope Ratio Analysis

Carbon and nitrogen stable isotope ratios were analyzed by the Stable Isotope Ratio Facility for Ecological Research (SIRFER) at the University of Utah. Samples collected in each year were pooled and single, multi-year averages (± 1 SE) were calculated for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each taxon. Increases in $\delta^{15}\text{N}$ values were considered increases in trophic status. There is a typical increase in $\delta^{15}\text{N}$ of 3‰ (DeNiro and Epstein 1981) and $\delta^{13}\text{C}$ of 1‰ (DeNiro and Epstein 1978) between predator and prey, resulting in a mean slope of three for trophic level increases when the δ values are plotted. Organisms that fell within these parameters were considered to be obtaining similar levels of benthic or pelagic carbon.

The proportion of pelagic carbon utilized by each taxa was estimated by plotting a line with a slope of 3 through the primary consumer for each of the benthic and pelagic components of the food web on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plane (as per Vander Zanden et al. 1999a and Post 2002). The pelagic and benthic primary producers were not used because seasonal variation makes them an unreliable base for a food chain plot (Zohary et al. 1994). *Daphnia* were used as the pelagic primary consumer and snails were used as the benthic primary consumer. The proportion of pelagic carbon utilized by each species was then estimated from the relative horizontal position occupied by each species between the pelagic and benthic lines. The trophic level occupied by each organism was calculated as per Hobson and Welch (1995) and

TABLE 1. Mean and standard error (SE) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each of the sample taxa. Sample sizes are included for each year of collection. Trophic level was calculated as per the equation of Hobson and Welch (1995) and using the $\delta^{15}\text{N}$ values of *Daphnia* as the pelagic primary consumer upon which all other trophic level calculations were based. Percent pelagic represents an estimate of the proportional abundance of pelagic carbon in each organisms diet (see text for calculation methods).

Sample	Abbrev.	n 1999	n 2000	$\delta^{13}\text{C}$ Mean (SE)	$\delta^{15}\text{N}$ Mean (SE)	Trophic Level	% Pelagic
Bryozoan	BR	0	1	-29.10 (0.00)	2.50 (0.00)	1.5	85
Sponge	SP	0	5	-29.28 (0.02)	2.82 (0.08)	1.6	82
<i>Sida crystallina</i>	SC	3	6	-28.93 (0.39)	3.56 (0.25)	1.8	84
Periphyton	PE	11	19	-22.75 (0.39)	4.16 (0.30)	2	0
Phytoplankton	PH	6	17	-28.36 (0.32)	4.18 (0.19)	2	100
<i>Daphnia</i> sp.	DA	10	14	-30.16 (0.35)	4.25 (0.27)	2	100
<i>Leptodiptomus ashlandi</i>	LA	0	2	-29.20 (0.20)	5.15 (0.05)	2.3	100
Zooplankton	ZP	4	0	-30.23 (0.08)	5.65 (0.22)	2.4	100
<i>Epischura nevadensis</i>	EN	1	7	-30.41 (0.77)	5.76 (0.06)	2.4	100
Snails	SN	4	0	-20.83 (0.49)	5.80 (0.21)	2.5	0
<i>Diacyclops thomasi</i>	DT	0	1	-29.20 (0.00)	5.80 (0.00)	2.5	100
Copepod	CP	6	0	-30.10 (0.10)	7.03 (0.12)	2.8	100
Chironomidae	CH	11	12	-25.21 (0.61)	7.31 (0.23)	2.9	56
<i>Leptodora kindti</i>	LK	5	4	-30.28 (0.18)	7.49 (0.36)	3	100
Corixidae	CO	3	3	-26.03 (0.12)	7.65 (0.37)	3	67
Smallmouth bass (YOY) <i>Micropterus dolomieu</i>	SB	3	0	-26.47 (0.17)	7.70 (0.12)	3	72
Aquatic Mites	AM	3	1	-26.70 (0.29)	9.13 (0.58)	3.4	79
Yellow perch (YOY) <i>Perca flavescens</i>	YPj	6	12	-27.39 (0.23)	9.33 (0.29)	3.5	88
Rainbow trout (Hatchery) <i>Oncorhynchus mykiss</i>	RTh	4	7	-25.44 (0.49)	9.84 (0.17)	3.6	67
Bridgelip sucker <i>Catostomus columbianus</i>	BS	0	2	-27.75 (0.35)	10.00 (0.60)	3.7	94
Carp <i>Cyprinus carpio</i>	CA	9	9	-25.34 (0.33)	10.23 (0.14)	3.8	68
Brook trout <i>Salvelinus fontinalis</i>	BT	4	3	-26.54 (0.67)	10.33 (0.43)	3.8	82
Kokanee (wild) <i>Oncorhynchus nerka</i>	KOW	3	3	-28.73 (0.23)	10.42 (0.23)	3.8	100
Rainbow trout (wild)	RTw	8	24	-26.35 (0.41)	10.43 (0.19)	3.8	80
Largescale sucker <i>Catostomus macrocheilus</i>	LS	7	12	-25.25 (0.08)	10.58 (0.03)	3.9	68
Whitefish <i>Coregonus clupeaformis</i>	WF	9	11	-29.09 (0.14)	10.61 (0.21)	3.9	100
Smallmouth bass <i>Micropterus dolomieu</i>	SB	5	17	25.79 (0.16)	10.85 (0.16)	3.9	76
Northern pikeminnow <i>Ptychocheilus oregonensis</i>	NP	3	9	-26.39 (0.36)	10.85 (0.31)	3.9	82
Sculpin (Cottidae)	SU	10	10	-25.81 (0.21)	10.97 (0.12)	4	77
Yellow perch (adult)	YP	7	12	-27.23 (0.18)	11.38 (0.34)	4.1	93
Kokanee (hatchery)	KOh	3	7	-25.40 (0.05)	11.50 (0.07)	4.1	73
Walleye <i>Stizostedion vitreum</i>	WA	10	33	-26.13 (0.11)	12.00 (0.15)	4.3	84
Burbot <i>Lota lota</i>	BU	4	13	-27.92 (0.08)	12.24 (0.14)	4.4	100

used the $\delta^{15}\text{N}$ value for *Daphnia* as the primary consumer in the food chain.

Results

Mean (and SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and the estimated trophic position, for each of the 33 taxa included in this study are presented from lowest to highest trophic position in Table 1. The position of each taxa on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plane is presented in Figure 2. The most important result for the purposes of this study was periphyton were considerably more enriched in ^{13}C than phytoplankton ($-22.8 \delta^{13}\text{C}$ versus $-28.4 \delta^{13}\text{C}$), which allowed us to distinguish benthic from pelagic food components of the food web (Figure 2). Given one can make this distinction among primary producers, and given food chain constituents are arranged on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plane along a line with slope of approximately 3 (DeNiro and Epstein 1981), there is a striking lack of exclusively benthic consumers in the Lake Roosevelt food web. Snails were the only organisms that our results identified as exclusive consumers of benthically fixed carbon (Figure 2). Although their position in Figure

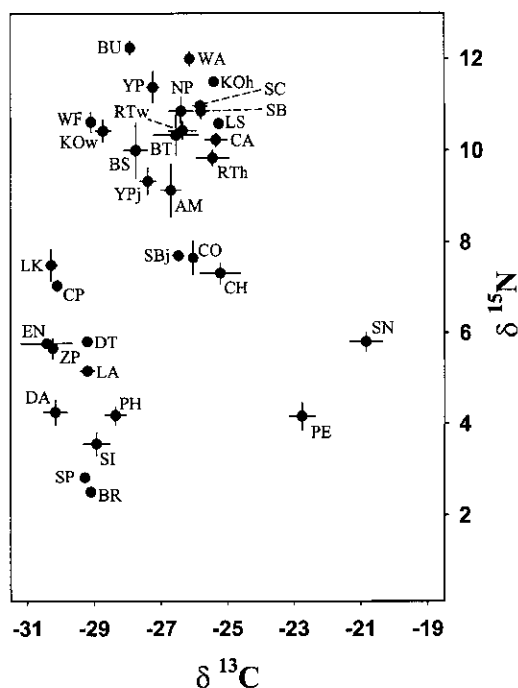


Figure 2. Stable isotope ratios for carbon ($\delta^{13}\text{C}$, ‰) and nitrogen ($\delta^{15}\text{N}$, ‰) for the food web components of Lake Roosevelt for 1999 and 2000. Table 1 provides a key to species abbreviations.

2 suggests heavy utilization of pelagic carbon, chironomids appear to rely upon benthic carbon sources for 44% of their diet. All other taxa, especially higher trophic level organisms, appear to collect the majority of their carbon from pelagically fixed sources (Figure 2).

The Lake Roosevelt aquatic community contains a rich pelagic component. The water flea *Daphnia* (including *D. schodleri*, *D. galeata*, *D. retrocurva*), and additional branchiopod *Sida crystallina*, and the calanoid copepod *Leptodiaptomus ashlandi*, were the pelagic herbivores that were abundant during the collection period. Their trophic level positions were estimated at 2.0, 1.8, and 2.3 (Table 1). The herbivorous branchiopod *Bosmina longirostris* may also be common in Lake Roosevelt, but abundances were too low during collection periods to permit inclusion in the study. Potentially predacious zooplankters included the calanoid copepod *Epischura nevadensis*, the cyclopoid copepod *Diacyclops thomasi*, and the large branchiopod *Leptodora kindti*. *Epischura* and *Diacyclops* both exhibited omnivorous diets with trophic level estimates that were approximately one-half trophic level above *Daphnia* (Table 1). The trophic level estimate for *Leptodora* was 3 (one full trophic level above *Daphnia*) and suggests an exclusively predacious diet and reliance upon *Daphnia* as a prey item. The pelagic vertebrate planktivores included wild kokanee (*Oncorhynchus nerka*) and lake whitefish (*Coregonus clupeaformis*). Their estimated trophic levels (3.8 and 3.9) suggest they primarily consume the larger predatory species of zooplankton. Burbot was observed as the top trophic level consumer, with the highest $\delta^{15}\text{N}$ value of any lake Roosevelt consumer (Figure 2), and 3.4 trophic levels above *Daphnia* (Table 1). The position of the exclusively pelagic animals in Figure 2 illustrates a linear structure with a slope of 2.6 ($P=0.035$) that spans more than two trophic levels. When examined by year, the pelagic taxa had a linear structure with a slope of 2.4 in 1999 ($P=0.004$), and a slope of 3.4 in 2000 ($P=0.011$).

All other organisms included in this study exhibit increased $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ suggesting at least partial inclusion of benthic carbon in their diet and increased trophic status when compared to the pelagic invertebrates. Existing at approximately the same trophic level as *Leptodora* were YOY smallmouth bass (*Micropterus dolomieu*), corixids, and chironomids (Figure 2), with chironomids

exhibiting a smaller portion of benthic carbon in their diet than either YOY smallmouth bass or corixids (Table 1). Aquatic mites held the highest trophic position among the invertebrate organisms (trophic level = 3.4): the relative importance of pelagic carbon in their diet was estimated at 79%. Young-of-the-year yellow perch occupied a trophic position similar to the aquatic mites (Figure 2) and pelagic carbon was estimated to comprise 88% of their diet (Table 1).

The majority of the fishes in Lake Roosevelt occupied fairly high trophic position (trophic level ≥ 3.6) and primarily utilize pelagic carbon (Table 1, Figure 2). Bridgelip sucker (*Catostomus columbianus*), carp (*Cyprinus carpio*), brook trout (*Salvelinus fontinalis*), kokanee (*Oncorhynchus nerka*), rainbow trout (*Oncorhynchus mykiss*), largescale sucker (*Catostomus macrocheilus*), whitefish (*Coregonus clupeaformis*), smallmouth bass, and northern pikeminnow (*Ptychocheilus oregonensis*) all possessed trophic level estimates between 3.6 and 3.9 (Table 1). Among these, kokanee and whitefish exhibited the largest utilization of pelagic carbon, and largescale sucker the least (Table 1). Those fishes observed to occupy the highest trophic positions in Lake Roosevelt included sculpins (*Cottus* sp.), yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), and burbot (*Lota lota*). Trophic position among these fishes ranged from 4 to 4.4, and utilization of pelagic carbon ranged from 77% (for *Cottus*) to 100% for burbot (Table 1).

Our estimates of the dietary contribution of pelagic carbon (Table 1) illustrate exceptionally little utilization of benthic carbon in Lake Roosevelt. Snails were the only organisms that appeared to rely exclusively on benthic carbon. All others appear to collect the majority of their carbon from pelagic sources. Chironomids exhibited the least utilization of pelagic carbon. Among the fishes, estimated consumption of pelagic carbon ranged from 68% to 100%. And for those fishes assumed to feed within the benthic portion of the food web (sculpin, carp, suckers) the lowest estimated proportion of pelagic carbon in the diet was 68% for carp and largescale sucker. Among the fishes listed above, the pelagic contribution to the diet averaged 77%, and was as high as 94% (for bridgelip sucker).

Although we fully expected to observe little benthic carbon utilization among the Lake Roosevelt organisms, a few unusual results are

noteworthy. We were surprised to see *Daphnia* and phytoplankton possessing identical $\delta^{15}\text{N}$ values suggesting they occupy similar trophic position (Figure 2). We were also surprised to observe sponges, bryozoans, and *Sida* with $\delta^{15}\text{N}$ values that were below the $\delta^{15}\text{N}$ values of phytoplankton (Figure 2). Additionally, if snails consume only periphyton, their $\delta^{15}\text{N}$ values should be enriched by approximately 3‰ over periphyton (Deniro and Epstein 1981). These anomalies may be a result of primary producers giving unreliable or questionable isotope signatures (Zohary et al. 1994). Both Vander Zanden et al. (1999a) and Post (2002) identify problems with primary producer isotope signatures and recommend using benthic and pelagic primary consumers as the base of their respective food chains when examining trophic relationships among higher trophic level organisms. Finally, there is no relationship whatsoever between the isotope signature of hatchery reared and wild salmonids. For both kokanee and rainbow trout, those of hatchery origin were more enriched in ^{13}C , and their estimated trophic level varied from the wild fish (Table 1, Figure 2).

Discussion

The first objective of this study was to determine the feasibility of C and N stable isotope analysis for observing the food web structure of Lake Roosevelt. Periphyton were significantly more enriched in ^{13}C than phytoplankton (Figure 2), which allowed us to distinguish between the two carbon pathways. The $\delta^{15}\text{N}$ values showed uniform stepwise enrichment in relation to the trophic status of organisms, especially in the pelagic portion of the food web (Figure 2). Together, the two isotope ratios indicate a system with a strong pelagic component and a diminutive benthic component in the aquatic food web. Lake Roosevelt supports a well defined pelagic component in the food web that consists of multiple trophic levels (Figure 2). Nitrogen isotopes demonstrated herbivorous, omnivorous, and carnivorous zooplankton (Table 1). The planktonic invertebrates provided the diet for wild kokanee and lake whitefish, and these fishes provided the primary prey source for burbot (Figure 2). Because there are organisms with exclusively pelagic diets having $\delta^{15}\text{N}$ values ranging from the lowest consumer to the top predator, we believe there is an adequate supply of pelagically fixed carbon in the reservoir. Given several species of benthic fishes are present in

Lake Roosevelt, if there were an adequate supply of benthically fixed carbon, there should have been organisms with exclusively benthic carbon signatures from the primary producer through the top consumer trophic level. However, the exclusively benthic component of the food web never extended beyond the primary consumer level (Figure 2). The stepwise shift away from a benthic diet and toward a pelagic diet with each trophic increase suggests that minimal levels of benthic carbon are fixed in the reservoir. The benthic carbon that is lost to metabolism and excretion with each trophic increase is replaced with the abundant pelagically fixed carbon, leaving a void in the food web plots in the region where higher level benthic consumers would be expected to be positioned by stable isotope theory (Figure 2).

Of the fishes typically considered to be obligate benthivores, all had isotope values indicating pelagic carbon in their diet (Table 1). Our most extreme example was bridgelip sucker, which had $\delta^{13}\text{C}$ values indicating 94% utilization of pelagic carbon. The degree to which the benthic fishes consumed benthically produced carbon varied, but it did not appear to make up more than 32% of the diet for any of them. Those fishes that were predicted to have an exclusively benthic diet did have carbon signatures indicating the highest reliance upon benthically produced carbon of any fishes in the reservoir (with the exception of hatchery fishes), yet the majority of their carbon intake was still from pelagic production. The reason for this is that there simply appears to be little benthic carbon in the overall Lake Roosevelt food web. Snails were the only organisms to have carbon signatures indicating an exclusively benthic diet (Figure 2). Stomach data collected from Lake Roosevelt by others has indicated all fishes have at least low levels of zooplankton in their diet (Baldwin and Polacek 2002). During our collection periods, largescale suckers and carp were witnessed swimming in the reservoir just below the surface, feeding on the abundant zooplankton. Since 1997 we have routinely observed largescale suckers feeding on the surface throughout the reservoir on nearly every occasion that we sampled fish (39–87 days per year). This suggests many fishes may adjust their feeding habits when their natural food source is not available.

Conflicting information exists between stomach content data and isotope data. Isotope data indicated that burbot were feeding primarily on

the planktivorous fishes, kokanee and lake whitefish (Figure 2). However, stomach data presented in Cichosz et al. (1998) indicates burbot diets do not include salmonids. Stomach samples had been collected primarily during late summer when the reservoir has returned to full pool. It is quite likely that the stomach data represent the snapshot in time phenomena where one receives a view of what the fish has eaten in the past few hours, but that is not necessarily representative of the overall majority of its diet. Burbot move into the shallows in the fall, at the same time kokanee move into the stream mouths to spawn. Burbot are suspected of preying heavily on kokanee at this time and we have collected several burbot with kokanee in their stomachs at these locations, which further conflicts with stomach data (Cichosz et al. 1998).

It was difficult to determine exactly what walleye were feeding on from the isotope data. According to their isotope ratios they could have been feeding on a combination of several fishes (Figure 2), which agrees with 1998 stomach data (Spotts et al. 2000) in which walleye had been observed to prey upon members of several fish families present in the reservoir. Although, no salmonids were found in walleye stomachs from the individuals collected for this study, walleye are thought to prey heavily on kokanee and trout in the reservoir (Baldwin and Polacek, 2002). We have pumped many kokanee and rainbows out of Lake Roosevelt walleye stomachs using lavage techniques. In some cases, individual walleye contained as many as 12 kokanee or rainbow trout.

Existing stomach content data suggest kokanee and lake whitefish had a 93% diet overlap in 1997 (Cichosz et al. 1998), which correlates well with isotope data (Figure 2). Cichosz et al. (1998) also report 91% diet overlap between kokanee and rainbow trout and a diet consisting of both pelagic and benthic prey. However, our isotope data indicate a much greater difference, and no benthic component in kokanee diets (Figure 2). Wild rainbow trout had $\delta^{13}\text{C}$ values that indicate their diets are composed of approximately 80% benthic prey (Table 1). This discrepancy, as with the one mentioned above for burbot, is perhaps an artifact of the stomach samples having been collected when benthic productivity is at its annual peak and the stomach contents only represent the organisms diet over the previous several hours. The stable isotope data conversely provide a long-term average

of the seasonal variation in the organisms diet. Here, it is likely the stomach data exaggerate the importance of benthic prey in kokanee diets.

The northern pikeminnow isotopic data placed it in the secondary consumer, mixed diet group which is lower than was predicted. The northern pikeminnow was once common in Lake Roosevelt and constituted up to 60% of the total gillnet catch in 1948 (Gangmark and Fulton 1949). However, the northern pikeminnow population has been steadily declining, with a gillnet relative abundance of 26% in 1965 (Earnest et al. 1966), 15% from 1980–1983 (Beckman et al. 1985), 6% in 1990 (Griffith and Scholz 1991), and <1% in 1996 (Cichosz et al. 1998). In the lower Columbia River system northern pikeminnow prey heavily on juvenile salmon and steelhead (Zimmerman and Ward 1999). The decline in the northern pikeminnow population in Lake Roosevelt has mirrored the rise in population of the introduced walleye, which was not recorded in gillnet catches until 1965. The walleye population increased to 29% of the relative abundance by 1980–1982 (Beckman et al. 1985), and has since leveled off in the range of 15–25% between 1988 and the present (Peone et al. 1991, Griffith and Scholz 1991, Cichosz et al. 1998). Vander Zanden et al. (1999b) used stable isotopes to examine trophic changes in aquatic food webs with the invasion of a competing predator. Lake trout in lakes with introduced smallmouth bass had more negative $\delta^{13}\text{C}$ values (-29.2‰ versus -27.4‰) and reduced trophic status (3.3 versus 3.9). The $\delta^{13}\text{C}$ values indicated a shift away from a diet of mostly fish to a diet of mostly zooplankton. The decrease in trophic status as determined from $\delta^{15}\text{N}$ values further indicates a shift to a zooplankton diet. Vander Zanden et al. (1999b) suggest that when bass are introduced to a lake system, they outcompete lake trout for forage fish, forcing the trout to a diet consisting primarily of zooplankton. The highly predacious nature of walleye (Francis and Vondracek 1990) may allow them to displace the northern pikeminnow. Northern pikeminnow diets typically consist of fish and benthic invertebrates (Wydoski and Whitney 1979, Simpson and Wallace 1982). If walleye outcompete pikeminnow for a fish-based diet, as indicated by $\delta^{15}\text{N}$ values, the pikeminnow is forced to rely more heavily on benthic invertebrates. The strongest competition between the two would most likely occur in the spring, prior to the arrival of a new

crop of YOY forage fishes. Northern pikeminnow would be forced to a diet consisting of their other prey item, benthic invertebrates. At the same time, however, benthic invertebrates are in short supply due to the drawdown. Isotope data have also suggest there is not enough benthic carbon to support secondary consumers, which may help explain the decline in the northern pikeminnow.

It is apparent that stable isotope analysis is sufficient for tracing broad carbon pathways in Lake Roosevelt, providing a view of the reservoir's overall food web structure. The high number of fishes in the mixed benthic-pelagic feeding group made it difficult to trace precise carbon pathways. To determine precisely what these fishes are feeding on, one would have to include stomach data. Stomach data will provide precise information on what an organism has eaten at one point in time, but as we have suggested, there can be conflicts between isotope data and stomach data taken from only one point in the year. Isotope data, coupled with stomach content data collected from several sample dates through the year would give the most precise view of carbon pathways in an ecosystem. Perhaps more importantly, although many of the large western storage reservoirs possess a diverse assemblage of what are considered benthic and pelagic fishes, our results suggest these aquatic systems are driven by pelagic carbon. Resource managers should be made aware of the detrimental impact water level fluctuations can have on the benthic component of aquatic food webs. Thus, in systems similar to Lake Roosevelt, those environmental factors which affect open water productivity are likely to impact the entire food web.

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Literature Cited

- Baldwin, C., and M. Polacek. 2002. Evaluation of limiting factors for stocked kokanee and rainbow trout in Lake Roosevelt. Unpublished annual report submitted to Spokane Tribe of Indians, Lake Roosevelt Fisheries Evaluation Program, Wellpinit, WA. Contract No. 94BI32148. Washington Department of Fish and Wildlife, Spokane, Washington.
- Beckman, L. G., J. F. Novotny, W. R. Parsons, and T. T. Terrel. 1985. Assessment of the fisheries and limnology in Lake F. D. Roosevelt 1980-1983. U. S. Fish and Wildlife Service. Unpublished final report to U. S. Bureau of Reclamation. Contract No. WPRS-0-07-10-X0216:FWS-1406-009-904. Seattle, Washington.
- Cabana, G., and J. B. Rassmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255-257.
- Cichosz, T. A., J. P. Shields, K. D. Underwood, A. T. Scholz, and M. B. Tilson. 1998. Lake Roosevelt fisheries and limnological research: 1996 unpublished annual report. U.S. Department of Energy, Bonneville Power Administration. Report No. DOE/BP-32148-2. Portland, Oregon.
- DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution on carbon isotopes in animals. *Geochimica Et Cosmochimica Acta* 42:496-506.
- DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution on nitrogen isotopes in animals. *Geochimica Et Cosmochimica Acta* 45:341-351.
- Ernest, D. E., M. H. Spence, R. W. Kiser, and W. D. Brunson. 1966. A survey of the fish populations, zooplankton, bottom fauna, and some physical characteristics of Roosevelt Lake: unpublished research report. Washington Department of Fish and Game. Fisheries Management Division, Olympia, Washington.
- France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series* 124:307-312.
- Francis, J. T., and Vondracek, B. 1990. Predator prey interactions of Lake Erie walleye: 1 July 1987-30 June 1990. Unpublished final report. Ohio Department of Natural Resources. Division of Wildlife. Columbus, Ohio.
- Gangmark, H. A., and L. A. Fulton. 1949. Preliminary surveys of Lake Roosevelt in relation to game fishes. U.S. Fish and Wildlife Service Special Science Report No. 5. Seattle, Washington.
- Griffith, J. R., and Scholz, A. T. 1991. Lake Roosevelt fisheries monitoring program: Annual report 1990. Prepared for: Fred Holm, Project manager. U.S. Department of Energy, Bonneville Power Administration. Report No. DOE/BP-19819-3. Portland, Oregon.
- Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relations within a high arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 84:9-18.
- Hobson, K. A., and H. E. Welch. 1995. Cannibalism and trophic structure in a high arctic lake: insights from stable isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1195-1201.
- Keough, J. M., M. Sierszen, and C. A. Hagley. 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography* 41:1135-1140.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Et Cosmochimica Acta* 48:1135-1140.
- Nigro, A. A., T. T. Terrel, and T. G. Beckman. 1981. Assessment of the limnology and fisheries in F. D. Roosevelt Reservoir. Unpublished annual report. Prepared for the U.S. Bureau of Reclamation, by the U. S. Fish and Wildlife Service, National Fishery Research Center, Seattle, Washington.
- O'Brien, W. J. 1990. Perspectives on fish in reservoir ecosystems. Pages 209-226 in K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors, *Reservoir Limnology*. John Wiley and Sons, New York.
- Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs* 27:55-112.
- Peone, T. L., A. T. Scholz, J. R. Griffith, S. Graves, and M. G. Thatcher. 1991. Lake Roosevelt fisheries monitoring program: unpublished annual report, 1989. U.S. Department of Energy, Bonneville Power Administration. Report No. DOE/BP-91819-1. Portland, Oregon.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293-320.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703-718.
- Simpson, J. C., and R. L. Wallace. 1982. *Fishes of Idaho*. University of Idaho Press, Moscow, Idaho.
- Spotts, J. V., J. P. Shields, T. C. Cichosz, and K. D. Underwood. 2000. Unpublished annual report, 1998. Lake Roosevelt fisheries monitoring and evaluation program creel survey and population analysis. Spokane Tribe of Indians. Department of Natural Resources. Prepared for the Bonneville Power Administration. Division of Fish and Wildlife. Portland, Oregon.
- U.S. Army Corps of Engineers. 2000. Water Management Division. Available online at www.NWD-WC.usace.army.mil/TMT/tdg-data/months.html
- Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rassmussen. 1999a. Patterns of food chain length in lakes: A stable isotope study. *American Naturalist* 154:406-416.
- Vander Zanden, M. J., J. M., Casselman, and J. B. Rassmussen. 1999b. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464-467.

- Weirenga, R. E., S. T. J. Juul, and W. H. Funk. 1997. Investigation into the primary productivity of Lake Roosevelt, Washington. Unpublished interim report. State of Washington Water Research Center, Pullman, Washington.
- Wilson, G. A. 1996. Nutrient and trophic state reduction in the Franklin D. Roosevelt Reservoir of Washington State. State of Washington Water Research Center, Pullman, Washington.
- Wydoski, R. S., and R. R. Whitney. 1979. Inland Fishes of Washington. University of Washington Press, Seattle, Washington.
- Zimmerman, M. P., and D. L. Ward. 1999. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River basin, 1994–1996. *Transactions of the American Fisheries Society* 128:995–1007.
- Zohary, T., J. Erez, M. Gophen. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. *Limnology and Oceanography* 39:1030–1043.

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